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THYLACODES – THYLACODUS – TULAXODUS: WORM-SNAIL NAME CONFUSION AND THE STATUS OF *SERPULORBIS* (GASTROPODA: VERMETIDAE)

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INTRODUCTION

In the worm-snail family Vermetidae, a large group of species (of still doubtful monophyly) is characterized by the absence of an operculum, the horny structure enabling other vermetids to fully or partially close the opening of the attached shell tube. Such species were traditionally described and grouped in the nominal genera *Serpulorbis, Lementina,* or *Thylacodes* (or variant forms of these names). Disputed authorships, numerous subsequent emendations, and conflicting type designations created a very complex situation, made worse by the introduction of similar sounding names such as *Thylacodus* and *Thylaeodus* for related, but not synonymous, taxa. With increasing involvement and mention of these vermetids in a wide range of biological studies, ranging from Recent and fossil diversity assessments to gene order research (e.g., Rawlings et al., 2001), taxonomic cleanup is urgently needed and the following note attempts to disentangle the confused situation.

TAXONOMY

The worm-snail genus *Tulaxodus* was formally introduced by Jean-Étienne Guettard (1770: 143 ff.) as "*Tulaxodus*, Tulaxode" with an extensive description of "caractere générique" as well as numerous vernacular references to recognizable published literature and illustrations. This work was usually cited by subsequent workers as dating from 1774, which is a slightly modified later edition with the same taxonomic content. Guettard's (1770/1774) work should not be confused with his earlier publications describing worm-snails and other tube-building animals entirely in the vernacular (1766a, b; reprinted in 1777a, b). Keen (1961: 191) considered Guettard's *Tulaxodus* unavailable because she viewed it as introduced in a non-binominal fashion in his 1774 publication. However, Guettard's name is available as of his 1770 publication, for the same reasons given by Bieler (1992: 16, 17) when arguing for the validity of *Tenagodus* dating from the same work. The name satisfies the requirements of ICZN (1999) Articles 11(4) (1), 11(5), as well as 12(1), and other names introduced in the work are likewise in current use, such as *Kuphus*, *Uperotis*, and *Brechites.*

Blainville (1828: 40) introduced the name *Tulaxoda* with the statement "Tulaxode [using Guettard's vernacular name]), Tulaxoda", followed by a page reference to Guettard's work (no year given) and a short description. *Tulaxoda* is not valid as a replacement name (because not citing the original name – ICZN [1999] Art. 33.2.1), but does qualify as a new description. No type species selection was found for it.

The name *Tulaxodus* was also subsequently modified to *Thylacodes*. The first to list it in this fashion appears to have been Agassiz (1846: 370, 381). His statement "Thylacodes – (V. Tulaxode Guett.)" was accepted as an emendation by Herrmannsen (1849: 575, 636), Newton (1891: 217), and Neave (1939–1940: 484). However, Agassiz only referred to Guettard's vernacular name and his "*Thylacodes*" was dismissed as a *nomen nudum* by Keen (1961: 191), an action here followed.

Herrmannsen (1849: 575, 636) accepted Agassiz's spelling of *Thylacodes* for Guettard's name, which he misspelled *Tulaxodes*, and cited a prior reference to Guettard's vernacular name "Tulaxode" (Deshayes, 1832: 1083) as well as Blainville's (1828) *Tulaxoda*. Herrmannsen's action is here accepted as a formal emendation of *Tulaxodus* to *Thylacodes*; his misspelling of Guettard's original name cannot be confused with any other name then in existence, especially since he provided an

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exact page reference to Guettard's original *Tulaxodus* in this context. The emendation from (now correctly spelled) *Tulaxodus* to *Thylacodes* was reiterated by Newton (1891: 217), who credited Agassiz (1846) and Mörch (1862, see following discussion). *Tulaxodes* was subsequently mentioned by various authors, for instance as "Tulaxodes, Guett." in synonymy of *Vermetus* by H. Adams & A. Adams (1854: 357), as "Tulaxodes, Guettard … 1774" in synonymy of *Thylacodes* "Guettard" by Mörch (1862: 65), and even as possibly related to belemnites, by Fleming (1837: 98). Paetel (1875: 218) synonymized *Tulaxoda* Blainville under "Tulaxodes Guett.", while considering the latter as the "current and correct" name for the group (1875: iv; here translated from the original German). Somewhere along the line *Tulaxodes* was probably intended as an emendation of *Tulaxodus* Guettard, but was not found formally introduced as such and is here treated as an incorrect subsequent spelling. Sacco (1896: 10) also addressed "*Tulaxodes* Guett. 1774" and stated he would have accepted its priority if the name had not been ill composed ("mal composto"). He accepted Agassiz's 1846 action as an emendation to *Thylacodes*, but considered that name junior to *Lemintina* Risso, 1826.

Lemintina Risso, 1826 (p. 114, also as *Lementina* in caption to pl. 2 on p. 432) was based, by monotypy, on *Lemintina cuvieri* Risso, 1826. Both spellings were subsequently used. The earliest (first reviser) choice was made by Herrmannsen (1849: 580, 581) who listed both names and used *Lemintina* instead of *Lementina,* but other authors continued employing *Lementina,* including Paetel (1875: 107, iv) who listed that spelling as "current and correct" (here translated from the original German). The identity of *L. cuvieri* remained a matter of discussion, with most authors interpreting the original figure as representing the large non-operculate vermetid of the Mediterranean. That species has been referred to by many names, including *Serpulorbis polyphragma* Sasso, 1827, and *Vermetus gigas* Bivona Bernardi, 1832. Many authors (e.g., Keen, 1961: 202) accepted *Serpula arenaria* Linnaeus, 1758, as the senior name for this species (a choice in conflict with parallel usage in teredinid bivalves – e.g., Zammit Maempel, 1993 – and a topic beyond the scope of this paper). H. Adams & A. Adams (1854: 359), for instance, placed *Lementina* with "?" in the synonymy of *Serpulorbis*, and stated "The genus *Lementina* of Risso is most probably a badly-observed and incorrectly-figured *S. arenaria*, an inhabitant of the Mediterranean." The stylized original figure of a living specimen (Risso 1826: fig. 16) appears to blend features of Vermetidae and serpulid polychaetes. Chavan (1944: 338) stated that the "coquille-type est une tube d'Annélide," and the remaining tube fragments in the Risso collection (MHNH Paris) labeled *L. cuvieri* were recognized as polychaete tubes by Arnaud (1978: 114). In any case, even if interpreted as a vermetid species, *Lemintina* would be a junior subjective synonym of *Thylacodes*, as explained below. *Limentina* is a misspelling also appearing in the literature (e.g., Suter, 1913: 259).

Mörch's (1862: 64 ff.) monographic revision of the group adopted Guettard's taxon as "Thylacodes, Guettard, 1774" – the form emended by "Agassiz" [i.e., Herrmannsen, 1849, see above] and used it as senior synonym of a group of several nominal genera, including *Serpulorbis* Sasso, 1827. *Serpulorbis* had been introduced by Sasso (1827: 483) with the type species, by monotypy, *Serpulorbis polyphragma* Sasso, 1827. The synonymy of Guettard's and Sasso's genera was widely accepted, an example being Newton (1891: 217), who treated *Serpulorbis* Sasso, 1827 in synonymy of *Thylacodes* "Guettard, 1770." As will be shown below, *Thylacodes* and *Serpulorbis* are objective synonyms sharing the same type species.

Keen (1961: 191), who viewed Agassiz's (1846) usage of the name *Thylacodes* as a *nomen nudum,* apparently did not consider Herrmannsen (1849), and accepted Mörch (1862: 64) as the first author who validly introduced this taxon (Mörch had credited *Thylacodes* to Guettard, but repeated Herrmannsen's mistake of listing the original name as "*Tulaxodes*," not *Tulaxodus*). Guettard's (1770) work introducing the genus did not associate nominal species (other than in the vernacular). Mörch (1862) included 21 nominal species in *Thylacodes*, but like all authors before him did not indicate a type species. Keen recognized the synonymy of *Thylacodes* "Mörch, 1862" with *Serpulorbis* Sasso, 1827, and she selected a type species that would make them objective synonyms: "*Serpulorbis polyphragma* Sassi, 1827 = *Serpula arenaria* Linné, 1758." As objective synonyms since 1961, *Serpulorbis* and *Thylacodes* can no longer be employed in a genus-subgenus relationship, as was done previously, for instance by Vaillant (1871).

Because Herrmannsen's (= Mörch's, = Newton's) *Thylacodes* is an emended form of

Tulaxodus, Keen's type species selection for *Thylacodes* also extends to the original *Tulaxodus*. Keen attempted to eliminate a junior synonym of *Serpulorbis* by assigning it the same type species by subsequent designation. This action, however, made *Thylacodes* the senior objective synonym.

In today's treatment (ICZN 1999 Art. 19.1), *Thylacodes* Herrmannsen, 1849, having been an unjustified emendation, would take its own author and date, and become a junior objective synonym of the original name, *Tulaxodus* Guettard, 1770. However, subsequent authors followed Agassiz, Herrmannsen, and Mörch, and the unjustified emendation *Thylacodes* became the form in prevailing use (prevailing usage is defined [p. 121 of the 1999 Code] as "usage …adopted by at least a substantial majority of the most recent authors concerned with the relevant taxon, irrespective of how long ago their work was published"). ICZN (1999 Art. 33.2.3.1.) states "when an unjustified emendation is in prevailing usage and is attributed to the original author and date it is deemed to be a justified emendation." Until Keen's (1961) mistaken declaration of *Tulaxodus* Guettard as a *nomen nudum*, the majority of authors used the form *Thylacodes* and attributed it to Guettard. *Thylacodes* is here accepted as a justified emendation of *Tulaxodus* (i.e., Art. 33.2.3.1 does apply) and dates from Guettard, 1770. Thus, *Thylacodes* Guettard, 1770, has priority over *Lementina/Lemintina* Risso, 1826 (if interpreted as a vermetid gastropod) and over *Serpulorbis* Sasso, 1827.

Although *Serpulorbis* Sasso, 1827, is the more commonly used name in the recent literature, "reversal of precedence" cannot be applied under ICZN (1999) Art. 23.9, because *Thylacodes* has been used as a valid name after 1899 (e.g., in the descriptions of *Thylacodes caperatus* Tate & May, 1900, and *Vermetus (Thylacodes) capensis* Thiele, 1925).

In addition, *Tulaxoves* appears in the literature (listed by Scudder 1882: I-346, II-330, who refers to Guettard "1 86" [sic]). It is here considered an incorrect subsequent spelling.

The nominal genus *Tulaxodus* and particularly its emendation *Thylacodes* should not be confused with the unfortunately very similar *Thylaeodus* and *Thylacodus,* both introduced by Mörch (1860a: 48 and 1860b: 77, respectively), and also genus-group names within this family. *Thylaeodus* (Mörch, 1860a: 48) was introduced for vermetids without columellar folds or lamellae discussed earlier in that paper ["pour les Vermets sans plis," as opposed to genus *Petaloconchus*, which has columellar shell lamellae]. Keen (1961: 191) selected as type species, by subsequent designation, *Bivonia contorta* Carpenter, 1857. To simplify matters, Keen (1961: 191) attempted making *Thylacodus* Mörch, 1860, a junior objective synonym of *Thylaeodus* by selecting the same type species, *Bivonia contorta* Carpenter, 1857, by subsequent designation. Keen referred to page 77 of Mörch's work, and stated he had originally included *Vermetus contortus* (Carpenter), *V. subcancellatus* Bivona Bernardi, *V. conicus* Dillwyn, and *V. contortus* var. *indentatus* Carpenter. However, *V. conicus* had not been included at all by Mörch, and *V. contortus* was indicated by a tentative "?". More importantly, on the following page Mörch (1860b: 78) clearly presented an original designation, here translated from the German original as "I therefore propose a subgenus *Thylacodus* for *Bivonia subcancellata* Biv., characterized by …". ICZN (1999) Art. 68.2 applies, and Keen's subsequent designation of a type species for *Thylacodus* Mörch is invalid.

The following is a summary of the genus-group names discussed in this article:

Lementina Risso, 1826 [a variant original spelling of *Lemintina*].

Lemintina Risso, 1826 [available name, selected over *Lementina* by first reviser action of Herrmannsen (1849); a junior subjective synonym of *Thylacodes,* if interpreted as a vermetid mollusk].
Type species: *Lemintina cuvieri* Risso, 1826.

Limentina [incorrect subsequent spelling of *Lemintina*].

Serpulorbis Sasso, 1827 [available name; a junior objective synonym of *Thylacodes*].
Type species: *Serpulorbis polyphragma* Sasso, 1827.

Thylacodes Guettard 1770 [available name; a justified emendation of *Tulaxodus* Guettard, 1770].
Type species: *Serpulorbis polyphragma* Sasso, 1827.

Thylacodus Mörch, 1860 [available name; a vermetid, but not congeneric with *Thylacodes*].
Type species: *Vermetus subcancellatus* Bivona Bernardi, 1832.

Thylaeodus Mörch, 1860 [available name; a vermetid, but not congeneric with *Thylacodes*].
Type species: *Bivonia contorta* Carpenter, 1857.

Tulaxoda Blainville, 1828 [available name; a junior synonym of *Thylacodes*].
Without designated type species.

Tulaxodes [incorrect subsequent spelling of *Tulaxodus*].

Tulaxodus Guettard, 1770 [available name, emended by justified emendation to *Thylacodes*].
Type species: *Serpulorbis polyphragma* Sasso, 1827, Vermetidae.

Tulaxoves [incorrect subsequent spelling of *Tulaxodus*].

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